The distribution of pond snail communities across a landscape: separating out the influence of spatial position from local habitat quality for ponds in south-east Northumberland, UK.

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Abstract.

Ponds support a rich biodiversity because the heterogeneity of individual ponds creates, at the landscape scale, a diversity of habitats for wildlife. The distribution of pond animals and plants will be influenced by both the local conditions within a pond and the spatial distribution of ponds across the landscape. Separating out the local from the spatial is difficult because the two are often linked. Pond snails are likely to be affected by both local conditions e.g. water hardness, and spatial patterns e.g. distance between ponds, but studies of snail communities struggle distinguishing between the two.

In this study, communities of snails were recorded from 52 ponds in a biogeographically coherent landscape in north-east England. The distribution of snail communities was compared to local environments characterised by the macrophyte communities within each pond and to the spatial pattern of ponds throughout the landscape. Mantel tests were used to partial out the local versus the landscape respective influences.

Snail communities became more similar in ponds that were closer together and in ponds with similar macrophyte communities as both the local and the landscape scale were important for this group of animals. Data were collected from several types of pond, including those created on nature reserves specifically for wildlife, old field ponds (at least 150 years old) primarily created for watering livestock and subsidence ponds outside protected areas or amongst coastal dunes. No one pond type supported all the species. Larger, deeper ponds on nature reserves had the highest numbers of species within individual ponds but shallow, temporary sites on farm land supported a distinct temporary water fauna. The conservation of pond snails in this region requires a diversity of pond types rather than one idealised type and ponds scattered throughout the area at a variety of sites, not just concentrated on nature reserves.

Introduction.

Ponds are a good example of a patchily distributed habitat. Wildlife that depends on patchy habitats has to cope with conditions and events within that patch, such as the physicochemical environment, resource availability and biotic interactions, and the surrounding landscape's potential influence on conditions within a patch and its effect on dispersal between patches. Studies of species distributions and abundance can find it difficult to separate out the importance of the events within a patch versus those processes operating in the wider landscape, e.g .Jeffries, (1998).

The biodiversity of ponds provides many examples, across the taxonomic spectrum from microbes to vertebrates, of local (sometimes called within- or intra- patch) and landscape scale effects. For example, survival of the Natterjack Toad (*Bufo calamita* L.) in individual ponds is determined by both the hydrological regime within a pond and dispersal from adjacent populations (Stevens and Baguette, 2008), while bacterial communities also show associations with environmental conditions within ponds but their dispersibility overcomes any spatial effects (Van der Gucht et al*.,* 2007). Pond invertebrates provide a wealth of evidence for the interplay of local and landscape influences - on populations and distributions, e.g. turnover of Notonectidae in between field ponds (Briers and Warren, 2000); on the importance of local environments for zooplankton within ponds even those that are interconnected, (Cottenie et al., 2003); and on the interaction of habitat within ponds and relative position of ponds for extinction and colonisation by insects (Jeffries, 2005a). Spatial patterns can arise from the interplay of life history characteristics and the landscape. For example Odonata with longer adult phases show stronger variation with landscape than those with short adult lives (Kadoya et al., 2008) whilst Van der Meutter et al., (2007), found different spatial outcomes for pond invertebrates with active versus passive dispersal strategies.

McAbendroth et al. (2005) demonstrated the importance of both local habitat, e.g. pond area, and distance between ponds upon the distribution of invertebrates from heathland ponds, with distance effects strongest up to ~4000m, although the effects varied with species' life histories. Briers and Biggs (2005) explained variations between invertebrate communities of ponds in Oxfordshhire, UK, separating out spatial effects defined by the distances between ponds from local habitat determined by physicochemical variables. Invertebrates showed significant variation with both influences, with positive correlations between pond communities up to 13km, though strongest up to 3.6km. Other studies of invertebrates have found little evidence of spatial effects with the communities dominated by local species sorting (Cottenie et al*.,* 2003 and Waterkeyn et al., 2008)

Spatial and temporal heterogeneity created by the mix of local and landscape influences, is an important characteristic of pond communities across a landscape (Talling, 1951; Jeffries, 1998; Williams et al., 2004). The striking variation of habitat between adjacent ponds results in a rich diversity of species at the landscape scale (β diversity) because, whilst the species richness within any one pond can be low, the cumulative species richness across many ponds is high (Williams et al., 2004). This variation creates a challenge for the conservation of pond biodiversity as the management of a few chosen sites cannot be relied upon to retain some transitory ideal (Jeffries, 2005b).

Whilst many studies have investigated the role of local and landscape factors on pond communities it is difficult to separate the two (reviewed Williams, 2006). In many cases the variation in local conditions such as pH or drying out, or presence of a predator will be determined by the environment of the surrounding landscape, e.g. land-use or geology, or the spatial position of the ponds relative to one another or colonisation history.

This problem is apparent in many studies of pond dwelling snails. Research into the distributions of snail communities has a long tradition of exploring both local and landscape influences, perhaps because of the evident importance of local physicochemical conditions. Water hardness and conductivity are particularly important (Boycott, 1936; Macan, 1950; McMillan, 1959; Aho, 1966; Powell and South, 1978; Pip, 1986; Lodge et al., 1987; Savage and Gazey, 1987; Costil et al., 2001; Briers, 2003). The primarily passive dispersal of snails is also likely to result in distinct spatial patterns, a long standing assumption (Darwin, 1859; Kew, 1893), although detailed information on dispersal of many invertebrates, including snails, is limited (Bilton et al., 2001; Bohonak and Jenkins, 2003). Connections between water bodies do allow active dispersal too, (e.g. Jurkiewicz-Karnkowska, 2008; Wilmer et al., 2008). Local factors may also include interactions with other species such as predation (e.g. by Odonata, Turner and Chislock, 2007), or physiological responses e.g. impacts from toxic cyanobacteria, (Gerard et al., 2008). Both local factors and landscape appear to be significant influences on the distribution and abundance of snails with many studies recognising that local and landscape factors are correlated (Pip, 1986; Lewis and Magnuson, 2000; Heino and Muotka, 2005, 2006; Jurkiewicz-Karnkowska, 2008) and that this problem is likely to affect results in other examples e.g. Antoine et al., 2004; Savage and Gazey, 1987. Other studies emphasise the role of chance colonisations (e.g. Klimowicz, 1959; Powell and South, 1978; Pip, 1986) as they show only weak relationships to local and landscape factors.

This study explicitly tests the relationship between pond snail communities in south-east Northumberland to both the local environments within ponds and the spatial distribution of ponds across the landscape, separating out their respective effects. The local conditions within each pond were characterised primarily by using the macrophyte plants within each pond. Macrophyte communities are good surrogates for a wide range of local environmental conditions e.g. physicochemical factors such as pH, nutrients and overall trophic status (Jeffries, 1991a; Costil and

Clement, 1996; Nicolet et al., 2004; Della Bella et al., 2008) and variations in habitat type due to local hydrology (Jeffries, 2008) or management (Jeffries, 1991a; Gee et al., 1997). Macrophytes are an important influence on snail communities, providing both physical habitat in which to live and varied surfaces from which snails can graze the periphyton. Snail diversity generally increases with increasing macrophyte diversity and some snails show specific associations with particular plants (Brönmark, 1985; Lodge, 1985; Lodge and Kelly, 1985; Kershner and Lodge, 1990; Underwood, 1991; Brown, 1997; Lewin and Smolinski, 2006). The influence of landscape scale factors was represented by the spatial distribution of the ponds, characterised by the distance between ponds. The similarity of snail communities was compared to variations of both macrophyte communities and distance between ponds.

Materials and Methods.

The region. All the ponds in this study were in south-east Northumberland, in northern England lying within a triangle from Amble in the north down to Newcastle airport in the south west and Whitley Bay in the south east, a north-south distance of 30km. The whole of this area has a consistent large–scale geography, climate and land-use as it lies within the Northumbria Coal Measures Natural Area, Natural Areas are regional sub-divisions of England, each one defined by wildlife, land-use and history which create a distinctive character (Natural England, 2008). Ponds are common throughout this area, including many on nature reserves and characteristic subsidence ponds over old coal mines (Beige, 2000).

Ponds. 52 ponds were sampled, 28 ponds in 2007, 24 in 2008, with all sampling taking place between May and early September, the season widely used in the UK for effective survey of freshwater plants (NRA, 1992). Ponds were chosen to include both obvious clusters and more isolated sites and also ponds with different origins and current management, in particular four types:

nature reserve ponds, subsidence ponds, old field ponds and coastal dune ponds. Ponds on nature reserves were created and managed for wildlife within the last 40 years, were often subject to planting up with macrophytes and are often visited e.g. children pond dipping. Subsidence ponds over old coal mines are widespread in the region, most forming in the last fifty years, many in farmland, not specifically managed and usually inaccessible to visitors. Old field ponds are defined by appearing on Ordnance Survey maps from the 1860s and are mostly livestock water sources. Coastal dune ponds were those within sand dune habitat and mostly unmanaged; we excluded those with tidal links to the sea. The most isolated pond was 2158m from the nearest other pond in the study (although within 210m of several lakes). The distribution of pair-wise distances between all the ponds sampled is shown in Figure 1, the greatest distance 29992m.

Sampling. Ponds were sampled for snails, macrophytes, pH and conductivity. The snails were recorded by sweeping vigorously for three minutes with a dip net (25x 25 cm frame, 0.5 mm mesh), the three minutes divided up between major sub-habitats as specified by the UK National Pond Survey protocol (Pond Action, 1993; tests of 3 minute sampling on ponds between 1 and 65 m^2 found no new invertebrate taxa after between 90 – 150 seconds, Jeffries; unpublished data). By allowing samples to stand in trays for five to ten minutes in the field, snails could gain a foothold, thus easing the task of finding small specimens. Many species could be identified in the field but uncertain specimens were brought into the laboratory for detailed examination with small individuals, including juveniles, grown on in aquaria and identified at a later date.

The Domin scale was used to record the extent of all plants within the boundary of pond as defined by the maximum winter water level (Pond Action, 1993). Most plants were recorded as species with the following exceptions due to difficulties of identification: all *Callitriche* species combined as Genus, *Agrostis stolonifera* L. and *Alopecurus geniculatus* L. combined as straggling grasses because vegetative growth could not be reliably separated. All filamentous algae were combined into one category.

Seasonal variation of snail numbers and plant abundance was likely to occur during the sampling period. Snails were recorded easily throughout the period, with obvious changes to numbers of individuals as juveniles appeared in the populations. Snails were recorded simply as presence/absence to capture the distribution of species rather than the seasonally variable populations. Plants grew through the period but dominant plants were well established by May and obvious through into October beyond the sampling period. Some plants growing as isolated individuals may have been missed.

Conductivity and pH were measured with five readings taken using Hanna portable probes throughout each pond. Pond area was based on the maximum winter extent while distance from pond to pond was measured between nearest edges. Both were measured using Google Earth Pro; area measures varied by $\pm$ 6%, (two test ponds, measurements = 10 per pond, the measures spread over three days to reduce authors' recollection of judgements made in the process) and distance by $\pm$ 0.7% (same test protocol).

Table 1 gives summary data for pond area, pH and conductivity.

Analyses. The relative importance of the local pond habitat (characterised by the plant communities) versus spatial position (characterised by the distances apart of ponds) on snail communities was tested using the Mantel test (Fortin and Dale, 2007). Firstly, Jaccard's index of similarity was used to compare the presence/absence of snails recorded from each pond to all the other 45 ponds (i.e. 46 in total) containing snails. Jaccard's index uses simple presence/absence data; whilst this gives equal weight to perhaps just one specimen of a snail recorded in a pond dominated by a large population of another species this is appropriate for the study exploring distributions, some of which may be rare accidents. The Mantel test was then used to test the relationship of the Jaccard's similarities to distance between ponds. Similarly, the plant communities within each pond were compared using

the Bray-Curtis index of dissimilarity with the Mantel test used to examine for any association between differences in plant communities and distance between ponds. The Bray-Curtis index allows the numerical variation of plants recorded by the Domin scale to be captured in the analyses. This was important because the plants were being used as surrogates for a wide range of local conditions and the plant data suggested that species which were dominant in and perhaps indicative of certain pond types and their local conditions were also widespread at much lower abundances throughout many ponds. For example *Eleocharis palustris* was found in 33 of the 46 ponds but at Domin level 5 or above (i.e. 11% cover or above) in only 17 of these. The Bray-Curtis index would emphasise the importance of these dominant species characteristic of particular ponds. Finally any association between the differences in snail communities (Jaccard's index) and between plant communities (Bray-Curtis index) were tested using the Mantel test.

The Mantel test relies on measures of difference, such as similarity indices or physical distance, therefore the precise relationships between individual species and environment and environmental influences are difficult to interpret directly. The pattern of snail distributions in relation to plant species was characterised using Canonical Correspondence Analysis, CCA, run on ECOM 3.1. Only plants that were recorded in at least 15 ponds were included in the CCA, this threshold again used to emphasise the importance of widespread, dominant plants which define particular pond types and their local environments.

A partial Mantel test was used, as by Fortin and Dale, (2007), to separate out the relationship between snail communities to the local environment as represented by the plants, and to the spatial position as represented by the distance between ponds. The influence of distance was factored out by regressing the snail Jaccard's indices and the plant Bray-Curtis indices against distance and storing the residuals. A Mantel test was then carried out on these residuals. Mantel tests were run on PC ORD 3.1

Results

Snails were found in 46 of the 52 ponds. There was no consistent character to the ponds lacking snails. Two were coastal dune lagoons with high conductivity (1567 and 5854 µS cm^{-1}) and plants characteristic of brackish influence, two were Victorian field ponds (one heavily overgrown with willow, *Salix* sp., the other in a farmyard with diverse flora), one a temporary subsidence pond and the sixth on nature reserve. Fourteen species of snails were recorded of which *Radix balthica* L. was the most widespread, found in 31 ponds, whilst the others were found in fifteen ponds or fewer (Figure 2). Most ponds with snails yielded 1-3 species with 7 the highest total (Figure 3). There was no significant relationship between number of snails species and pond area or conductivity, including those ponds lacking snails (Figure 4, species:area plot). Regression results for number of snail species against pH gave weak negative relationship (r^2 = 7.9%, P<0.05). Of the eighty-two plant taxa recorded (including the combined species) most are widespread species in the region (Swan, 1993) but there were regional rarities sampled, including: *Bidens tripartita* L., along with species that are more typical of upland Northumberland (e.g. *Menyanthes trifoliata* L.) and the invasive *Crassula helmsii* (T. Kirk) Cockayne. All of the rarities, out of place species, and invasives were recorded from ponds dug on protected areas specifically for nature conservation.

Results from the full Mantel tests showed that the similarity of snail communities decreased significantly with increasing distance between ponds (Table 2) with a marked decline beyond 1000m and perhaps at shorter distances although the data are more limited (Figure 5a). The similarity of plant communities also decreased significantly with distance (Table 2, Figure 5b). The full Mantel test comparison of snail and plant communities showed that the differences between snail communities increased significantly as differences in plant communities also increased (Table 2). This is a good example of the problem of separating the effect of distance from the effect of the local environment i.e. the plants may be influencing the snails but also could be simply acting as a

surrogate measure of distance between ponds, since the plant versus distance Mantel test showed a significant relationship.

The partial Mantel test result which compared the snail and plant communities, having factored out distance, showed a significant relationship between snail and plant communities with differences in the snails between ponds increasing as differences in the plant communities increased (Table 2). Combining the results from the Mantel tests shows that differences in snail communities increase with both distance between ponds and variation in plant communities i.e. both distance and plants matter.

The CCA ordination depicting the relationships between the distribution of snails and widespread plants is shown in Figure 6. The cumulative variance captured by axes 1 and 2 was very low (axis 1 12.2%, axis 2 8.3%. The addition of pH, conductivity and area data still gave very low explanation (axis 1 15.8%, axis 2 12.1%), but distinct associations occur between snails and plants. The snails *Aplexa hypnorum* L. and *Galba truncatulata* (O.F. Müller), characteristic of temporary ponds, were associated with plants of temporary pools e.g. *Glyceria fluitans (L.) R. Br.*. The snails *Potamopogyrus antipodarum* (Gray) and *Hydrobia ulvae* (Pennant) were associated with plants characteristic of shallow coastal dune sites. *S*nails such as *Planorbarius corneus* L., *Anisus vortex* L. and *Physa fontinalis* L. which occur in larger, deeper inland sites are associated with *Typha latifolia* L., *Lemna minor* L. and *Juncus effusus* L.. Snails such as *Radix balthica* and *Gyraulus albus* (O.F. Müller), which are able to establish in a wide range of pond types, showed no strong relationships with any of the plants.

Discussion.

The snail communities distributed across the ponds were typical of lowland northern England with both the mean number of species per pond (mean 2.44) and the range (0-7 species) rather lower than that found in ponds and allied systems further south in the UK or Europe (e.g. Costil, 1994

mean snail species per pond = 4.2; Costil et al., 2001, 3.3; Brönmark, 1985, 7.9; Jurkiewicz-Karnkowska, 2008, 8.0; Pip, 1986 4.3). The widespread occurrence of *Radix balthica* combined with a long list of much less frequent species is typical of such ponds (McMillan, 1959; Costil, 1994; Michalik-Kucharz, 2008). The North east of England has a more limited snail fauna than further south, which may also reflect under recording (Kerney, 1999). Several species found in this survey are scarce in the region (*Bithynia tentaculata* L., *Planorbis planorbis* L., *Planorbis carinatus* (O.F. Müller), *Anisus vortex* and *Gyraulus crista* (L.) and the records of *Aplexa hypnorum* are the furthest north for England, although the species does occur occasionally in Scotland (Kerney, 1999).

The results of the Mantel tests showed that differences in the snail communities between ponds are associated both with the local habitat within the pond, characterised by the plants, and with distance between ponds across the whole landscape, supporting the general conclusion of McAbendroth et al. (2004) and Briers and Biggs (2005). The further apart ponds are the greater the differences in snail communities while similarly, the more plants differ between ponds the greater the differences in the snails. Both the plants and the distance will have direct effects on the snails but also act as surrogate data for other factors. For example, distance will directly influence snail distributions as snails are more likely to be carried to adjacent ponds by vectors or perhaps through occasional flood links, distance is also likely to reflect changing landscapes and land-uses. In this study the more northerly ponds were closer to the coast, mostly amongst farmland, wetland reserves or dunes whilst the more southerly were amongst peri-urban farms and human settlement. Different land-uses are likely to cause differences in the physicochemical environment within ponds (Briers and Biggs, 2005) although we do not have the data to explore such links in this study. For example conductivity may reflect water hardness. Jeffries (1991b) surveyed 50 ponds in the region, including several included this study, and found a significant correlation between conductivity and alkalinity (r^2=0.311, P<0.05) but higher conductivities in the current survey were found in the ponds along the coast containing plants associated with saline influence. Nor did pH and conductivity add greatly to the low levels of explanation in the CCA. The lack of extensive data for the

physicochemical environment of each pond restricts the detail with which we can explain the patterns of snail distributions. We can however demonstrate patterns of distribution that reflect both local and spatial influences even if the precise causes remain unclear. Plants will influence snails directly by providing different architecture and periphyton substrate but are also likely to reflect other local factors such as hydroperiod or water chemistry and physicochemical variation caused by adjacent landuse.

The spatial effects demonstrated for the snail communities in this study contrast to the apparent unimportance of spatial factors for other pond invertebrates when compared to species sorting within the pond (e.g. Cottenie et al., 2003; Waterkeyn et al., 2008). This may be an example of differences between taxa, the ponds in their studies being dominated by active dispersers, or taxa with ubiquitous egg banks. Pond snails (and many plants which lack seed banks or similar propagules) may be much more constrained by spatial factors.

The association of particular snails and plants shown by the CCA (Figure 6) suggests this is the case. For example the snails *Aplexa hypnorum* and *Galba truncatulata*, both of which are commonly found in temporary ponds, ditches and tracks (Kerney, 1999), were associated with the grasses *Glyceria fluitans, Agrostis stolonifera, Alopecurus geniculatus* and also *Ranunculus aquatilis* L.*,* all of which are common in temporary wetlands in Northumberland. These snails were missing from nearby permanent ponds offering different local environments. These ponds were generally deeper and dominated by mixtures of emergents such as *Typha latifolia* L. and submerged *Potamogeton* species which commonly supported *Radix balthica, Gyraulus (Gyraulus) crista* and *Gyraulus (Gyraulus) albus*, all three of these species are regarded as widespread in England and able to thrive in a wide range of habitat types (Kerney, 1999). The association between the snails *Bithynia tentaculata*, *Planorbis carinatus*, *P. planorbis*, *Anisus vortex*, *Planorbarius corneus* and *Physa fontinalis* and the plants *Typha latifolia*, *Lemna minor* and *Juncus effusus* (Figure 6) may be an example of confounding between local and landscape factors as these plants were more abundant in the southerly, inland ponds

where these snails are also clustered. Large and small ponds in this cluster suggest the proximity of ponds had allowed the snails to colonise all adjacent sites as these contained the species *Planorbarius corneus* and *Physa fontinalis* which were not found elsewhere. It is likely that the position of ponds across the study region and the land-use adjacent to each pond affect the physciochemical conditions within each pond (e.g. nutrients, hardness), so the plants may be simply a surrogate for other influences for which we lack the data. Local and landscape factors are interlinked; the purpose of this study was to test if both are important in their own right and the results of the Mantel tests show that they are both significant.

The outcome of the combined local and landscape influences is the high β diversity across the region, even though most ponds supported only small numbers of snail species. There were no single pond types or sub-areas which supported the full range of species and communities. Whilst the ponds with the highest numbers of snail species were on nature reserve sites some other ponds on reserves yielded no snails. The shallow grassy ponds with *Aplexa hypnorum* and *Galba truncatulata* were not on reserves but part of dense pond clusters created by land subsidence on farms or amongst dune hollows. The regional biodiversity of pond life requires a variety of pond and lake habitats, not just one idealised type (Declerck et al., 2005; Jeffries, 2005b; Bilton et al., 2009). Freshwater gastropods have suffered numerous extinctions, their vulnerability attributed in part to their lack of vagility restricting their ranges and opportunities to recover (Strong et al., 2008). The results from this study demonstrate that both the quality of local habitat and the distribution of ponds across the landscape are important for the sustainability of a diverse pond snail fauna.

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Table 1. Summary data for ponds in survey.

	Mean ± standard deviation	Minimum	Maximum
pH	7.2 ± 0.79	6.0	10.6
Conductivity, µS cm	1028 ± 931	157	5854
Area, m^2	1357 ± 1892	3	9665

Table 2. Results from the full and partial Mantel tests. The full Mantel tests compared similarity of the snail communities measured by Jaccard's index, the plant community dissimilarity measured by Bray-Curtis index and the distance between ponds. For the partial Mantel test the influence of distance was removed by regression of the snail or plants' respective indices against distance between ponds and then used the residuals for the Mantel test.

Test	Standardised Mantel statistic, r.
Full Mantel test	
Snail similarity vs. distance between ponds	-0.180, P < 0.01
Plant disimilarity vs. distance between Ponds	0.304, P < 0.001
Snail similarity vs. Plant dissimilarity	-0.368, P < 0.001
Partial Mantel test	
Snails vs. plants.	-0.335, P < 0.001

Figure labels.

Figure 1. The distribution of pair-wise distances between the study ponds.

Figure 2. The frequency with which each snail species was recorded from the 52 ponds in this study.

Figure 3. The distribution of snail species richness across all ponds.

Figure 4. Species:area plot for number of snail species against $\log_{10}$(pond area), area measured as maximum winter extent of pond.

Figure 5. Summary of snail and plant similarities over distances between ponds. (a) Snail mean Jaccard's index of similarity ± 1 standard deviation, (b) plant mean Bray-Curtis dissimilarity index ± 1 SD. Distances between ponds have been grouped into Log_{10}distance categories, the x axis labels showing the bottom threshold for the category. The first four categories are shown as grey columns because of the relatively small numbers of samples within these four ranges.

Figure 6. CCA biplot for the snails against plants. Note that only plants occurring in at least 15 ponds were used in the analysis. Snails are shown by black squares, species coded by abbreviated names as follows in bold ***A**plexa **hypn**orum, **G**alba **tru**ncatulata, **H**ydrobia **ulvae**, **P**otamogopyrus **ant**ipodarum, **G**yraulus **cri**sta, **G**yraulus **alb**us, **L**ymnaea **sta**gnalis, **P**hysa **fon**tinalis, **P**lanorbis **pla**norbis, **P**lanorbarius **cor**neus, **A**nisus **vor**tex, **P**lanorbis **car**inatus, **R**adix **bal**thica and **B**ithynia **ten**taculata.* Plant vectors are coded by abbreviations show here by underlining *Glyceria fluitans, Ranunculus aquatilis, Agrostis/Alopecurus, Rumex spp., Eleocharis palustris, Juncus articulatus, Myosotis scopriodes, Alisma plantago-aquaticum, Polygonum amphibium, Juncus effusus, Lemna minor* and *Typha latifolia.*

Figure 1.

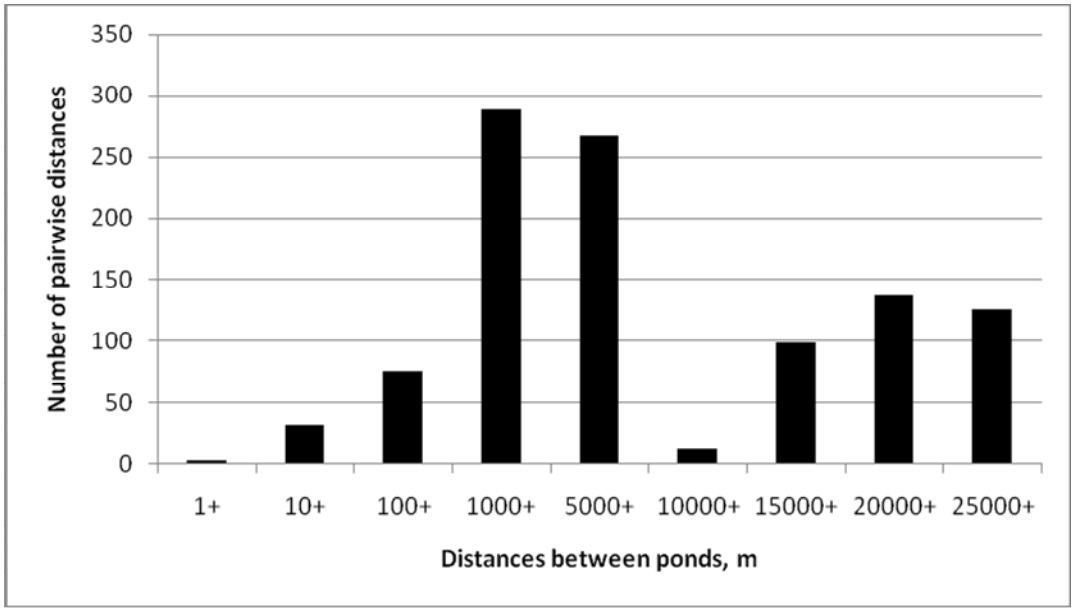
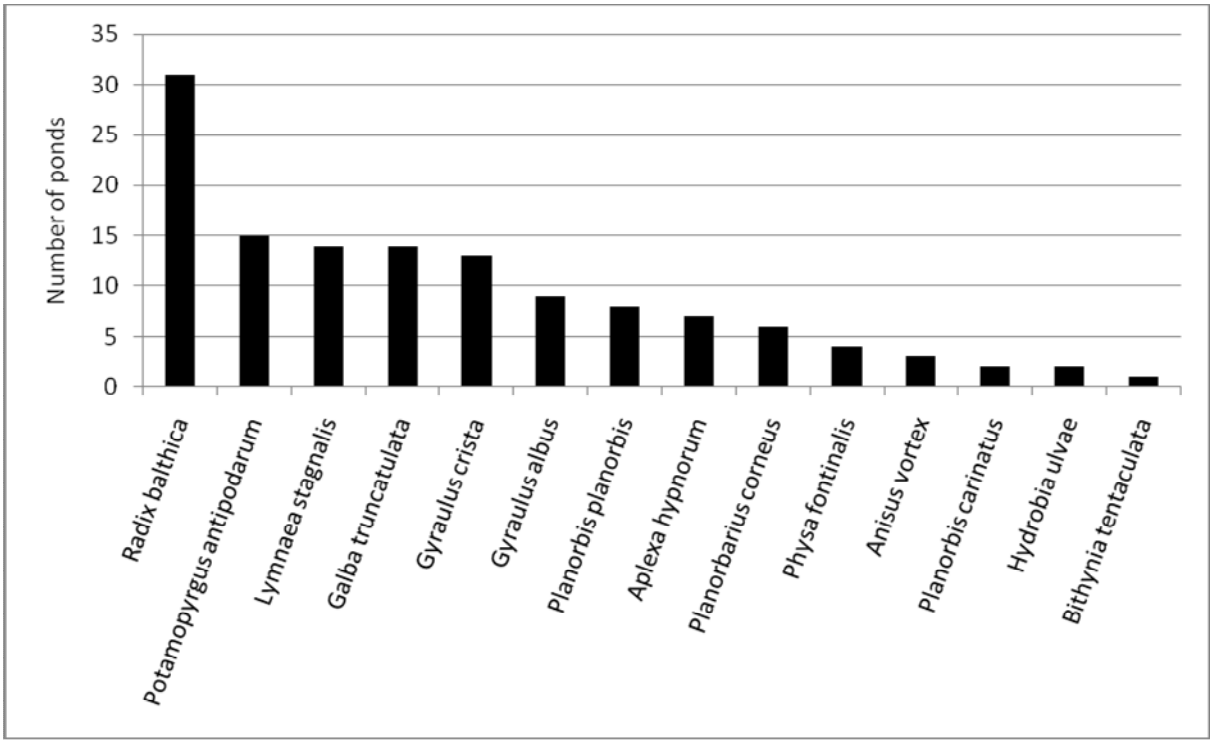

350
300
250
200
150
100
50
0
Number of pairwise distances
1+
10+
100+
1000+
5000+
10000+
15000+
20000+
25000+
Distances between ponds, m

Figure 2.


Number of ponds
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30
25
20
15
10
5
0
Radix balthica
Potamopyrgus antipodarum
Lymnaea stagnalis
Galba truncatulata
Gyraulus crista
Gyraulus albus
Planorbis planorbis
Aplexa hypnorum
Planorbarius corneus
Physa fontinalis
Anisus vortex
Planorbis carinatus
Hydrobia ulvae
Bithynia tentaculata

Figure 3.

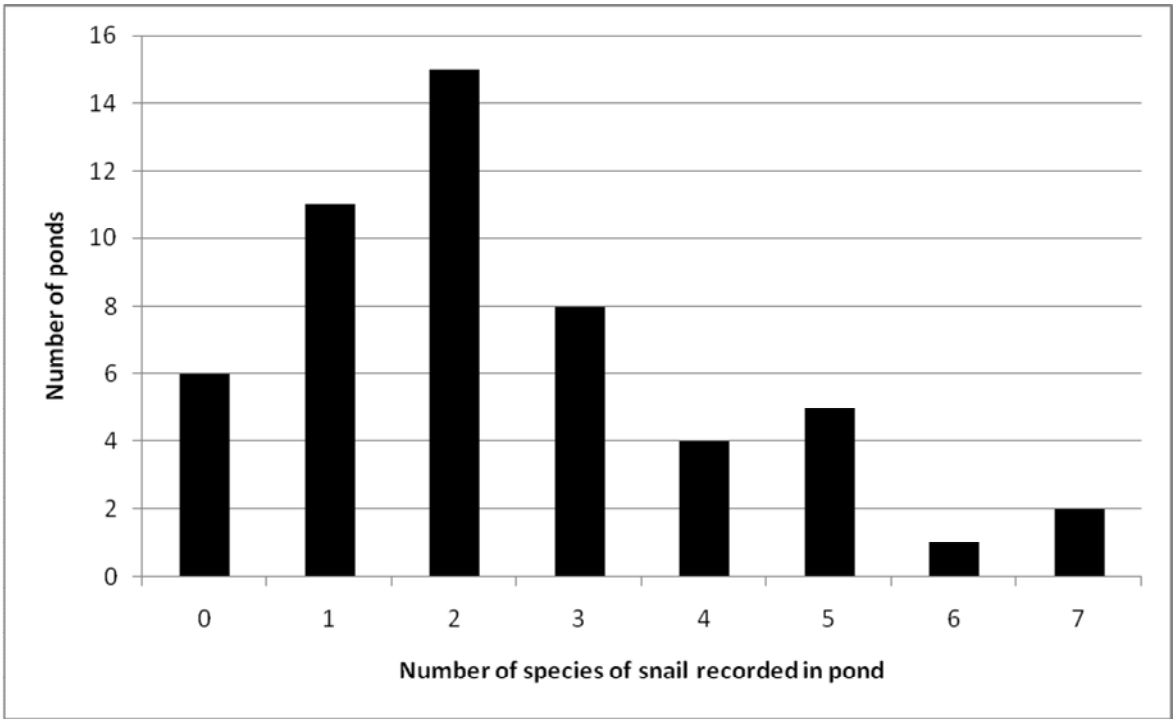

16
14
12
10
8
6
4
2
0
Number of ponds
0
1
2
3
4
5
6
7
Number of species of snail recorded in pond

Figure 4.

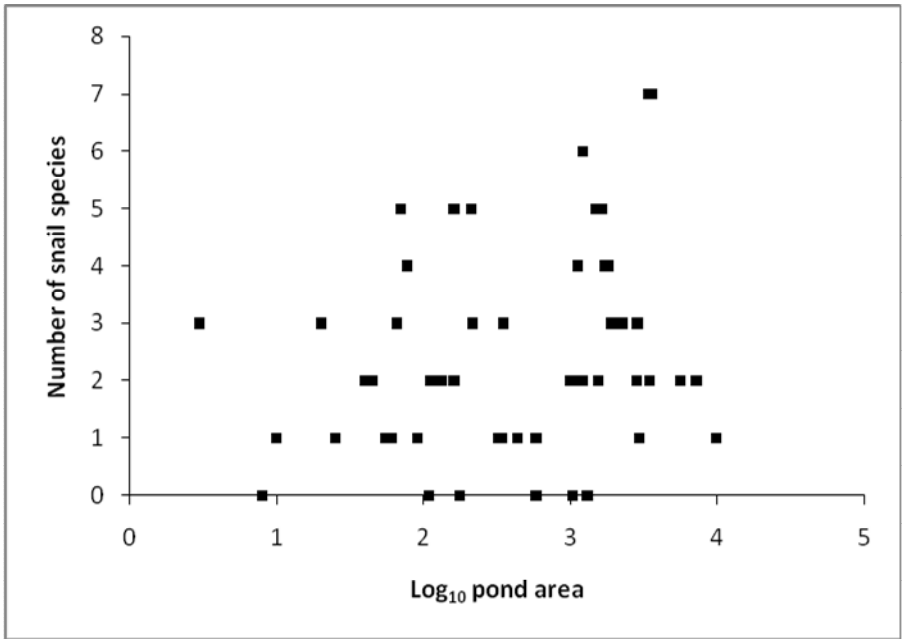
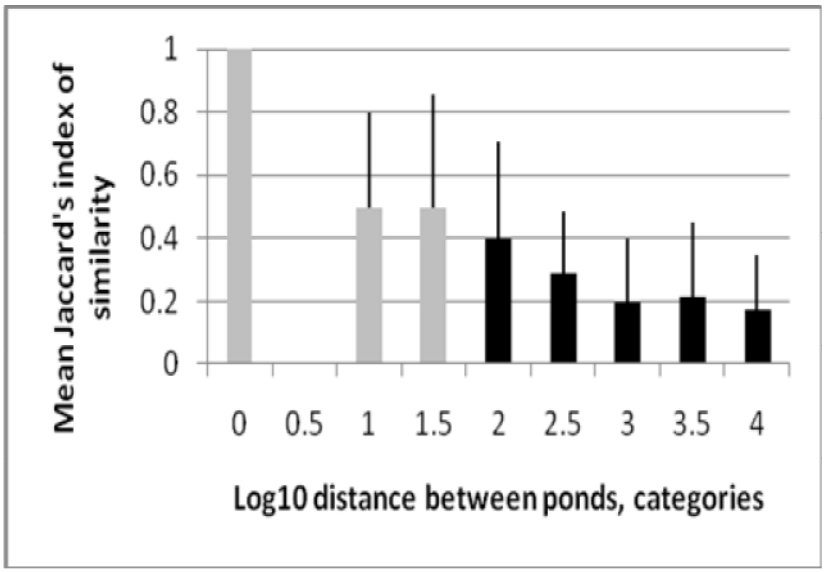


Figure 5 (a) and (b).



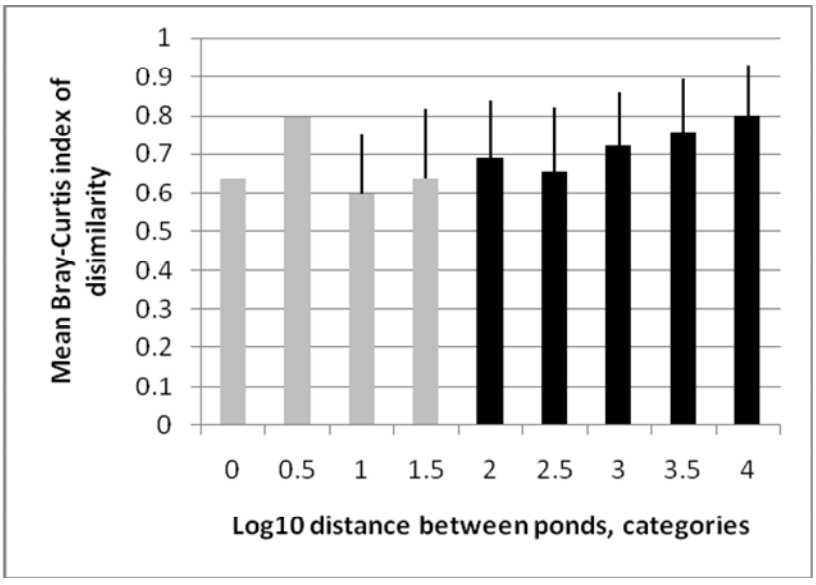
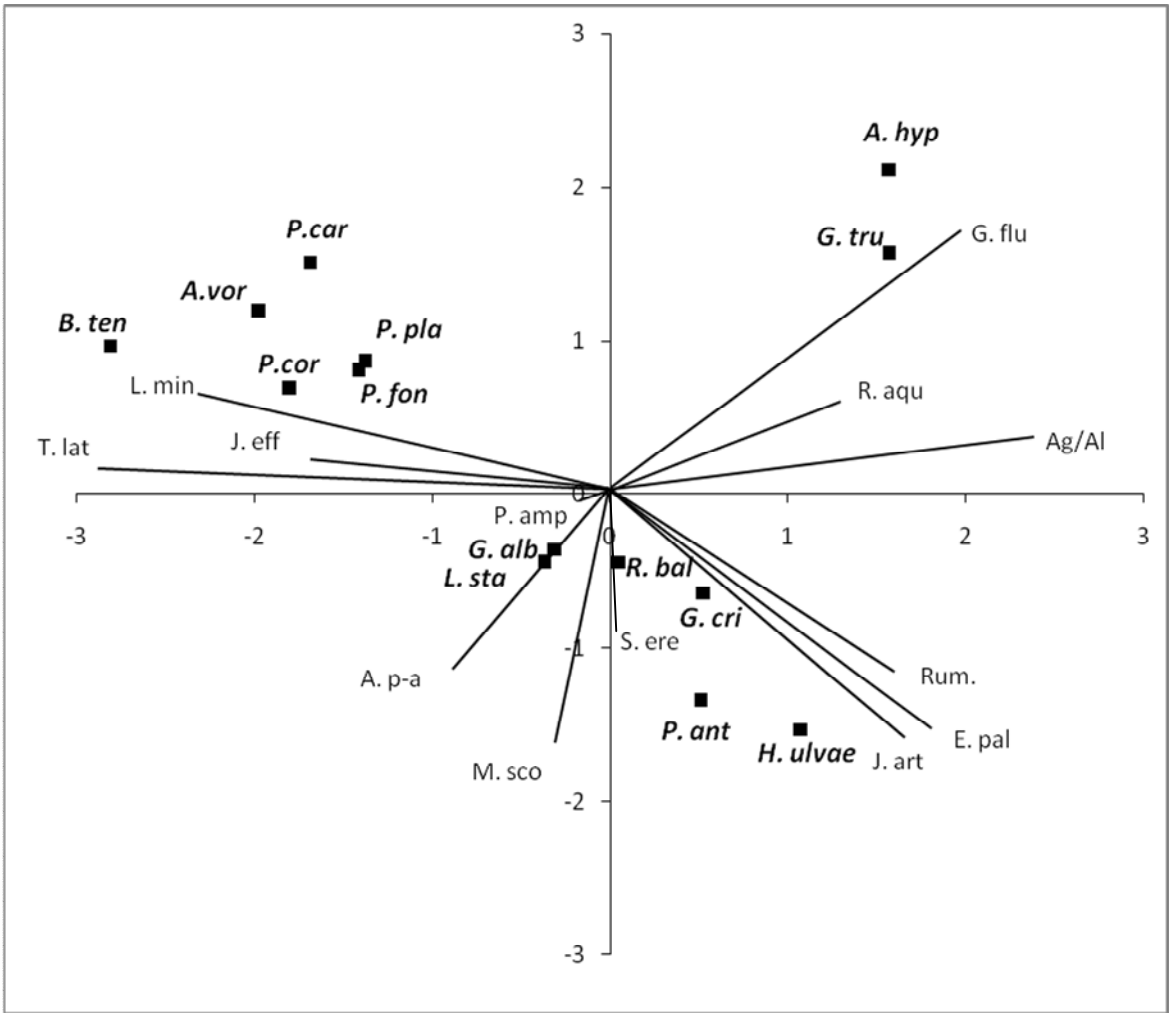


Figure 6.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3
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G. tru
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P.car
A.vor
B. ten
P. pla
P.cor
P. fon
L. min
R. aqu
T. lat
J. eff
Ag/Al
P. amp
G. alb
L. sta
R. bal
G. cri
S. ere
A. p-a
Rum.
P. ant
H. ulvae
J. art
E. pal
M. sco